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NESTING SUCCESS OF THE PROTHONOTARY WARBLER IN THE UPPER MISSISSIPPI RIVER BOTTOMLANDS

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ABSTRACT.—In 1993 and 1994, I studied the breeding biology and nesting success of Prothonotary Warblers (*Protonotaria citrea*) at the margin of the species' breeding range on the upper Mississippi and Black rivers in west-central Wisconsin. During the severe flooding of 1993, nesting success was reduced to a third of the level recorded in 1994, a more typical year. The rate of Brown-headed Cowbird (*Molothrus ater*) parasitism was the highest (26.9%) yet reported. House Wrens (*Troglodytes aedon*) were observed destroying only one nest, but they were suspected of having a larger role in nest failure as has been found in other studies (Walkinshaw 1938). *Received 30 Mar. 1995, accepted 21 Sept. 1995.*

The Prothonotary Warbler (*Protonotaria citrea*) is a secondary cavity nester that breeds in floodplain forests of the eastern U.S. Between 1966 and 1987, it experienced regional population declines in the southern U.S. (James et al. 1991) and in the northern Midwest (Graber et al. 1983). It is listed as one of ten area-sensitive warbler species (subfamily *Parulinae*) (Robbins 1979). Much of its floodplain forest habitat has been lost or degraded since presettlement times (Fredrickson 1979), and mangrove and riparian forests of Latin America used by the Prothonotary during the non-breeding season (Skutch 1989) are being rapidly destroyed or converted to other uses (Terborgh 1989). In the center of its breeding range in the southern U.S., less than 25% of the original bottomland forest remains (Fredrickson 1979, Harris et al. 1984). In Wisconsin, only 8% of presettlement floodplain forest remains in moderate to high quality condition (Mossman 1988).

Population monitoring of the Prothonotary Warbler across its breeding range is hampered by the inaccessibility of bottomland forests. In Wisconsin, where this study was conducted, there has been only one occurrence of a Prothonotary Warbler on all Breeding Bird Survey (BBS) routes from 1966 to 1991 (USFWS, unpubl. data), even though the species breeds commonly in suitable habitat (Mossman 1988). Furthermore, brood parasitism by the Brown-headed Cowbird (*Molothrus ater*) may be contributing to population declines by reducing productivity.

Several studies have examined the nesting ecology of the Prothonotary Warbler (Walkinshaw 1938, 1939, 1941, 1953; Petit 1986, 1989; Blem and Blem 1991, 1992). However, the majority of nests in these studies were built in artificial nest boxes. Use of artificial nest boxes may affect

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breeding parameters such as clutch size and nesting success (Mertens 1977), although preliminary studies do not support the hypothesis that nest box size affects clutch size for this species (C. Blem, pers. comm.). Hole nesting birds using nest boxes may also suffer artificially reduced rates of predation (Nilsson 1984, 1986, Moller 1989) as compared to nests in natural cavities. Conversely, the greater conspicuousness of nest boxes may increase predation rates compared to natural cavities. The diameter of a nest box entrance may also discourage or prevent cowbird parasitism. Few data exist on nesting success and brood parasitism rates for naturally occurring nests. The reproductive ecology of the Prothonotary Warbler has not been studied in detail in the upper Mississippi River region. I present here nest site characteristics, reproductive success, and rate of cowbird parasitism for Prothonotary Warblers nesting in the upper Mississippi River. This study also provides some insight into the effect of extreme flooding on the reproductive success of Prothonotary Warblers in this region.

STUDY AREA AND METHODS

I collected nesting data at three sites along a 113-km section of the Mississippi River in west central Wisconsin during 1993 and 1994 (Fig. 1) (pools 5–9, elevations 664–625′ asl, 44°09′N, 91°48′W, 43°31′N, 91°14′W). In this area, the river ranges from 1.3–4.0 km wide with numerous forested islands 0.25 to 300 ha in size. The river is bordered by steep bluffs dominated by oak forest (*Quercus* spp.) with patches of remnant prairie on steep south-facing slopes. Beyond the bluffs lie broad areas of agricultural land with scattered woodlots where there was once hardwood forest, savanna, and open prairie (Emlen et al. 1986). Riparian habitat occurs on islands and in strips 0.1 to 1.5 km wide on either shore of the river. Eastern cottonwood (*Populus deltoides*) and black willow (*Salix nigra*) are found on new alluvial deposits (Olsen and Meyer 1976). Older alluvial sites and mesic areas are dominated by silver maple (*Acer saccharinum*), green ash (*Fraxinus pennsylvanica*), river birch (*Betula nigra*), box elder (*Acer negundo*), and basswood (*Tilia americana*). American elm (*Ulmus americana*), once a dominant canopy species, is now represented only by saplings and young trees, larger trees having succumbed to Dutch Elm disease. Dominant understory plants include woodbine (*Parthenocissus inserta*), wood-nettle (*Laportea canadensis*), jewelweed (*Impatiens capensis*), violet (*Viola* spp.), poison ivy (*Rhus radicans*), button bush (*Cephalanthus occidentalis*), and grape (*Vitis* spp.) (Olsen and Meyer 1976).

Information on nesting Prothonotary Warblers was also collected at two sites along the lower portion of the Black River, two and seven km above its confluence with the Mississippi River. Floodplain vegetation along the lower Black River is similar to that on the Mississippi River (Barnes 1991). From mid-June to the end of July 1993, both the Mississippi River and the Black River experienced record-breaking floods which were directly responsible for numerous nest failures.

From mid-May to the end of July 1993 and 1994, I found nests by walking or canoeing through promising habitat and by following singing males. I recorded the location and stage of nesting along with characteristics of the nest and site. I returned to check each nest approximately every four days. I calculated nest success according to procedures in Mayfield (1961, 1975) and Caccamise (1977). Nest height was the distance from the ground to the

FIG. 1. The location of five study sites along the upper Mississippi River and the lower Black River.

bottom of the cavity opening, and only data from nests that had solid ground under them for some part of the nesting period were used (Table 1). Ratios of the number of young hatched to the number of eggs laid (H/E) and the number of chicks fledged to the number of young hatched (F/H) were used as indices of breeding success (Caccamisc 1977). The Mayfield (1961, 1975) method for calculating nest success adjusts for the stage at which a nest is first discovered.

TABLE 1
NEST PARAMETERS OF PROTHONOTARY WARBLERS IN THE UPPER MISSISSIPPI RIVER BOTTOMLANDS

Parameter	1993	1994
No. nests[a]	22	20
No. eggs	90	73
No. hatched	41	23
Hatched/egg	0.46	0.32
No. fledged	25	22
Fledged/hatched	0.61	0.96
No. successful nests	10	6
Percent successful[b]	45	30
Mayfield estimate[c]	0.20	0.66

[a] Nests include only those found during egg incubation stage.
[b] Success = fledged at least one young.
[c] Success calculated using Mayfield's (1961) correction for exposure. Estimate includes all nests (1993: N = 28; 1994: N = 32) found during incubation and nestling stages and represents probability of nest surviving through both stages.

RESULTS AND DISCUSSION

The three greatest sources of mortality for eggs and nestlings during this study were flooding, predation, and destruction by House Wrens (*Troglodytes aedon*). These were also the principal sources of nest mortality in Michigan (Walkinshaw 1938, 1953). Flooding was devastating in 1993 since the "hundred year" floods coincided precisely with peak nesting activity in mid-June. In 1993, 36% of all nests were flooded, while none was lost to flooding in 1994. No nests were abandoned during this study. Increased predation rates associated with observer nest visits are unlikely, since most nests were located over water, nest visits were brief, and a variety of non-terminal routes were used when visiting a nest.

Of 43 nests for which monitoring began during the incubation period, only one was observed being destroyed by a House Wren. In this case, the House Wren punctured all four eggs in an unattended nest and dropped one into the water below the nest. It is possible, based on their abundance and aggressive habits, that House Wrens were responsible for other losses attributed to predation.

Mean clutch size (4.31, Table 2) was smaller than that reported by Petit (1989, $\bar{x}$ = 4.75, N = 120), Walkinshaw (1941, $\bar{x}$ = 5.62, N = 118), or Blem and Blem (1992, $\bar{x}$ = 4.38, N = 266). Mean tree stub diameter at nest height in this study was greater (29.9 cm) than in Petit's (1987) study (13.6 cm). Prothonotary Warblers use cavities excavated by other birds as well as naturally occurring cavities. Many nests were found in cavities

TABLE 2
CHARACTERISTICS OF PROTHONOTARY WARBLER NESTS

Characteristic	N	$\bar{X} \pm SD$
Mean clutch size[a] (eggs)	36	4.31 ± 0.79
Nest diameter opening (cm)		
Least		2.5
Greatest		9.8
Mean	74	5.0 ± 1.35
Mean nest height above ground[b] (cm)	43	219.4 ± 124.3
Mean stub diameter at nest height (cm)	76	29.9 ± 13.7

[a] Nests included are only those found during incubation.
[b] Nests from 1993 were not included because all nests were found over highly fluctuating water levels.

that had been expanded through decomposition, and these accounted for the larger diameter openings.

Prothonotary Warblers glean arthropods from the ground and shrub layer of riparian forests. While the Prothonotary Warbler is not an obligate ground forager, it does use the shrub layer extensively when foraging, and the absence of this layer during much of the 1993 breeding season may have influenced foraging efficiency.

The record-breaking floods along the Mississippi and its tributaries in 1993 were largely responsible for the lower nest success in 1993 compared with 1994. Peak flood levels occurred precisely during the height of breeding activity for Prothonotary Warblers in June. The Mississippi River near Merrick State Park, Wisconsin (Fig. 1, Sites #1, #2) rose nearly 3 m between June 16 and June 26 (U.S. Army Corps of Engineers 1993). Although no data were available on water levels at study sites on the Black River, I noted similarly dramatic rates of rise. The Prothonotary Warbler typically nests within 2–3 m of the water's surface (Harrison 1975).

Picman et al. (1993) found that nest predation near marshes decreased with increasing water depth. Unusual flood waters may have made some nests less accessible to predators, thus decreasing nest losses from predation in 1993. The percentage of nests depredated in this study (27.6%, N = 28 from 1993 only) was lower than in Walkinshaw's (1941) study (41%, N = 27) but higher than in Petit's (1989) study (20.9%, N = 191). If nests lost to flooding are removed from the pool of nests available to predators, a predation frequency similar to Walkinshaw's (1941) is generated (44.4%, N = 18 from 1993 only). No attempt was made to distinguish predation losses from other nest losses in 1994. Most of Petit's nests were in artificial nest boxes with entrance holes smaller than the mean of the entrance holes in this study, which may have influenced predation rates in that study. Such nest box-specific effects on nest success will depend on the material used to construct the box (e.g., cardboard vs wood). House Wrens were absent from Petit's (1989) and Walkinshaw's (1941) Tennessee sites while they were common on Walkinshaw's (1941) Michigan sites and in this study. The presence of House Wrens may explain the similar predation rates for non-flooded nests in Michigan and Wisconsin, while the absence of House Wrens on the Tennessee sites may account for the lower predation rates reported by Petit (1989).

Potential nest predators observed in this study included Common Grackle (*Quiscalus quiscula*), Blue Jay (*Cyanocitta cristata*), House Wren, Common Crow (*Corvus brachyrhynchos*), gray squirrel (*Sciurus carolinensis*), and mink (*Mustela vison*). Species known to prey on Prothonotary Warbler nests include the gray squirrel (Walkinshaw 1938) and mice of the genus *Peromyscus* (Guillory 1987). Other likely predators in the study area include the raccoon (*Procyon lotor*), striped skunk (*Mephitis mephitis*), fox squirrel (*Sciurus niger*), and opossum (*Didelphus virginianus*). Although no snakes were seen in 1993, they were seen seven times in 1994 and have been reported as predators in other studies of Prothonotary Warblers (Petit 1989). Excluding the single nest destroyed by a House Wren, I was able to identify the predator of a nest by teeth marks in only three cases. Squirrels (*Sciurus* spp.) gnawed through the side of a total of three cavities in both live and dead trees. One such nest contained three Prothonotary Warbler eggs and five cowbird eggs and was located on a small island (<1 ha) isolated by approximately 200 m of swift and deep (>5m) floodwaters and had no dry land on it. Clearly, islands do not provide complete safety from tree-climbing terrestrial predators.

Nests were often placed in severely rotted trees in relatively exposed areas over water where they are vulnerable to damage from storms and wave action from boats. Of 76 nests in snags and stubs, none was lost due to the collapse of the tree, although two nest trees collapsed within one week after the warbler's fledging.

The incidence of cowbird parasitism was the highest yet reported (Table 3). A comparison of regional cowbird populations indicates that Midwest cowbird abundance is 2.5 times greater than in the eastern U.S. and is increasing (Robbins et al. 1986). The bottomland forests of the upper Mississippi are in agricultural lands that provide foraging habitat for cowbirds. Petit's (1989) Tennessee study was conducted in a riparian zone within a mostly forested landscape. These different land-use patterns may partly explain the higher parasitism rates in this study. Since Walkinshaw's (1938, 1941) studies in Michigan, cowbird populations have in-

TABLE 3
RATES OF COWBIRD PARASITISM OF PROTHONOTARY WARBLERS IN THE UNITED STATES

Location	No. nests	% Parasitism	Reference
Iowa	70	25.7	Norris (1890)
Michigan	28	10.7	Walkinshaw (1938)
Louisiana	57	12.3	Goertz (1977)
Illinois	154	15.6	Graber et al. (1983)
Tennessee	128	20.3	Petit (1989)
Wisconsin	67	26.9	This study (1996)
Virginia	998	0.013	Blem, unpubl. data

creased across the eastern U.S. This population increase could be partly responsible for increased parasitism rates since Walkinshaw's time.

Belles-Isles and Picman (1986) noted that House Wrens poke holes in eggs of other species within their territories, often removing the pecked eggs and disturbing the nest lining. Although I observed House Wrens destroying only one nest, Walkinshaw (1941) reported that 25% of 413 Michigan Prothonotary eggs and chicks were destroyed by House Wrens. Walkinshaw spent more time observing nesting behavior than I did during this study, giving him more opportunities to identify the cause of egg and nestling loss.

It has long been assumed that cavity-nesting birds are limited primarily by the availability of nest sites (Hilden 1965, Scott 1979, Mannan et al. 1980) and that House Wrens benefit from nest-destroying behavior by freeing up nest sites and perhaps decreasing foraging competition. Several studies have observed that Prothonotary Warblers often compete unsuccessfully for cavities with House Wrens (Smith and Dumont 1944, Graber et al. 1983). In Walkinshaw's (1941) comparative study of Prothonotary Warblers nesting in Michigan and Tennessee, he attributed comparatively lower nesting success in Michigan to competition from and nest destruction by House Wrens, a species not common on his Tennessee sites.

In a trial nest-box study conducted in 1994, we placed 20 wooden nest boxes within past Prothonotary Warbler breeding habitat. House Wrens occupied 16 (80%) of the nest boxes, and Tree Swallows (*Tachycineta bicolor*) nested in three (15%). No Prothonotary Warblers nested in the boxes.

House Wrens were the most abundant bird species in the study sites, as measured by point counts conducted during the study (Flaspohler 1994), and are common and widespread in floodplain forests throughout Wisconsin (Mossman 1988). I found numerous nests with missing eggs and with both disturbed and undisturbed nest linings. Because of the House Wren's habit of removing nesting material from the nests that it destroys (Belles-Isles and Picman 1986), and thereby disturbing the nest, one cannot confidently conclude that a disturbed nest implies a mammalian predator as proposed by Best (1978) and Petit (1989). Where no cowbird parasitism was present, I attributed the disappearance of eggs and nestlings to predation. Where House Wrens are abundant, this method may tend to overestimate predation rates and underestimate House Wren nest destruction rates.

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